Anthropocene 24 (2018) 61–71

Contents lists available at ScienceDirect

Anthropocene

journal homepage: www.elsevier.com/locate/ancene

Humans and climate as designers of the landscape in Serra da Bocaina National Park, southeastern Brazil, over the last seven centuries

Maria Carolina Guarinello de Oliveira Portes[a,b,c,*], Hugh Safford[d,e], Hermann Behling[a]

[a] University of Göttingen, Albrecht-von-Haller Institute for Plant Sciences, Department of Palynology and Climate Dynamics, Germany
[b] Instituto Chico Mendes de Conservação de Biodiversidade (ICMBio), Brazil
[c] CNPq-Brazil Scholarship, Brazil
[d] USDA Forest Service, Pacific Southwest Region, Vallejo, California, USA
[e] Department of Environmental Science and Policy, University of California, Davis, California, USA

ARTICLE INFO

Article history:
Received 20 April 2018
Received in revised form 11 November 2018
Accepted 12 November 2018
Available online 15 November 2018

Keywords:
Campos de altitude
Araucaria forest
Atlantic Forest
Human impact
Conservation
Palaeoecology

ABSTRACT

Campos de altitude and *Araucaria* forest are unique and highly diverse ecosystems and focus areas for conservation and restoration in southeastern Brazil. This paper reports a high-resolution paleoecological study of an approximately 700-year Late Holocene core, a period that includes the influence of two highly distinct civilizations and the transition between them: Amerindian/pre-Columbian and European/post-Columbian. Results highlight the interworkings of regional climate change and local human agency in "designing" the Late Holocene forest-grassland mosaic in the Serra da Bocaina. Amerindians maintained more open highland habitats probably through slash and burn agriculture. The depopulation of the study region after European arrival in the 1500s plus increasing precipitation led to a marked and rapid rebound in forest cover. After 1720 CE, establishment of permanent European communities and farming in the study area led to forest loss and a renewed expansion of grassland. Based on current knowledge about forest-grassland relationships, and in light of projections for warmer and wetter conditions in southeast Brazil, we provide suggestions for management strategies that might better maintain the mosaic of *Araucaria* forest and campos de altitude in the southeastern Brazilian highlands.

© 2018 Elsevier Ltd. All rights reserved.

1. Introduction

The Atlantic Forest biome occupies 1,300,000 km^2 of coastal and eastern Brazil, stretching from 3 °N latitude to almost 34 °S. Due to centuries of exploitation, only 10–15% of the Atlantic Forest biome remains in a natural or semi-natural state (Fundação SOS Mata Atlântica/ INPE - Instituto Nacional de Pesquisas Espaciais, 2017). The biome is one of the most diverse in the world, and is considered among the most important and most imperiled biodiversity hotspots on earth (Myers et al., 2000). It includes a mosaic of different ecosystems, including shoreline forests, lower, middle and upper montane rainforest, *Araucaria* forest, and campos de altitude (high elevation grass- and shrublands). Present at higher elevation, *Araucaria forest* has been reduced to <13% of its original distribution (Ribeiro et al., 2009), and campos de altitude are naturally restricted to small areas on the summits of the higher peaks and plateaux. One of the best preserved stretches of the Atlantic Forest is found between the highly populated metropolitan areas of São Paulo and Rio de Janeiro. Preservation here was promoted by mountainous topography and establishment of the firsts national park in South America (Itatiaia 1937, Serra dos Órgãos 1939). In 1972, the Serra da Bocaina National Park (SBNP) was added to the system to protect 100,000 ha of highly threatened forest on the south flank of the Serra do Mar.

Amerindians probably arrived in southeastern Brazil about 10,000 years ago (Figuti et al., 2004). They settled originally along the coast, but migrations and cultural transitions led a greatly increased human footprint in inland forests by 1800 yr BP (Noelli, 2008). By the time Portuguese settlers arrived in Brazil beginning in 1500 CE, centuries of swidden agriculture had altered much of the lowland forest, but the low population densities and primitive technologies of the Amerindians left some forest areas untouched and most cultivated areas were in some stage of recovery at any given time (Dean, 1995; Drummond, 1997). The first permanent Portuguese coastal settlements were built in SBNP beginning in the late 16th century, however inland colonization in the Paraíba do Sul valley dates from the early to mid-17th century (Nehren et al., 2013). The region experienced a number of economic cycles after Portuguese

* Corresponding author at: Abteilung Palynologie und Klimadynamik, Untere Karspüle 2, 37073, Göttingen, Germany.
E-mail address: maria-carolina.portes@icmbio.gov.br (M.C. Guarinello de Oliveira Portes).

https://doi.org/10.1016/j.ancene.2018.11.004
2213-3054/© 2018 Elsevier Ltd. All rights reserved.

settlement, including coffee plantations which were the main cause of forest loss inland of SBNP (Dean, 1995; Drummond, 1997).

Since the Last Glacial Maximum (LGM), there has been high temporal variability in the structure and distribution of ecosystems in southeastern Brazil. Behling et al. (2007) studied Late Pleistocene and Holocene vegetation development in the SBNP spanning the period 18,570 cal yr BP to 1280 cal yr BP. The climate was cold and dry in the Late Pleistocene, with frequent frost during winter months, and the landscape was dominated by campos de altitude with forests in lower elevation, protected locations, for example along streams. Arboreal pollen became much more common in the Holocene, comprised mainly of species from *Araucaria* forest, but it is clear that large areas of grassland persisted at upper elevations (Behling et al., 2007). Charcoal is found throughout the 17,000 year record, demonstrating that the highland flora was subjected to periodic fire and that the extent of fire adaptations in the flora cannot be attributed to recent anthropogenic fire alone (Behling et al., 2007; Safford, 2001). The greatest expansion of forest occurred during the Late Holocene ($\sim$ 4200 BP to present, Walker et al., 2012) when wetter conditions were established, resulting in a mosaic of campos de altitude, *Araucaria* forest and Atlantic Forest (Behling et al., 2007; Behling and Pillar, 2008). Many studies document the maximum expansion of *Araucaria* forest in southeastern and southern Brazil after 1500 CE, supporting the hypothesis of increasing effective moisture in the Late Holocene (Behling, 1995, 1997, 2007; Behling et al., 2004; Behling and Safford, 2010; Jeske-Pieruschka et al., 2010, 2012). At the same time, continued expansion of *Araucaria* in southern Brazil after 500–1000 CE during a period of slightly drier climate suggests an important role for human dispersal as well (*Araucaria* was a major staple of the indigenous diet) (Bitencourt and Krauspenhar, 2006; Robinson et al., 2018).

A major question is the relative extent to which climate and humans have influenced ecosystem conditions in the Americas since human arrival at the beginning of the Holocene. It was long presumed that pre-Columbian human influence on ecosystem status and distribution in the Atlantic Forest was minimal (Drummond, 1997; Guidon, 1992). However, science continues to uncover more and more evidence of extensive and sometimes intensive influence of pre-Columbian cultures on ecological conditions in southern and southeastern Brazil (Noelli, 2000; Robinson et al., 2018). Here we focus on the spatial and temporal relationships between *Araucaria* forest and campos de altitude on the Bocaina Plateau over the last seven centuries, a period that includes the influences of two highly distinct civilizations and the transition between them: Amerindian and post-Columbian. Late Holocene, current, and future trends of atmospheric warming and increasing effective moisture favour continued forest expansion. We use high-resolution paleoecological data to discern the conditions under which campos de altitude have been maintained in the Serra do Mar highlands, in the face of forest expansion and at altitudes that are lower than the climatic treeline. Campos de altitude and *Araucaria* forest are both unique, diverse ecosystems and focus-areas for conservation and restoration in southeastern Brazil. In this contribution, we seek (1) to disentangle the influences of climate and humans on the changing status of the forest-grassland mosaic in the Serra da Bocaina during the Late Holocene; and (2) to provide a foundation for better understanding how the grassland component of the mosaic might be conserved under a future climate that will greatly favour forest expansion.

2. Environmental setting

2.1. Geomorphology

Our study area is located on the Bocaina Plateau in the SBNP (22°44′02.0″ S, 44°38′39.4″ W, 1539 m a.s.l.) at the border of São Paulo and Rio de Janeiro states in southeastern Brazil (Fig. 1). Topographic relief is related to tectonic events resulting from the western Gondwana breakup and the opening of the South Atlantic Ocean throughout the Cretaceous, followed by reactivation of Proterozoic shear zones and uplift during the Late Cenozoic (Hiruma et al., 2012; Siqueira Ribeiro et al., 2011). The Bocaina Plateau, the highest part of this section of the Serra do Mar, is a remnant erosional surface, mostly underlain by decomposed Proterozoic gneisses and granites (Ab'Saber, 2003; Hiruma et al., 2012). Colluvium are common at the bases of slopes on the Bocaina Plateau and are normally characterized by a sandy or clayey matrix (Hiruma et al., 2012). Carbonate bearing rocks are absent in the region. Overall the landscape is characterized by rounded mountaintops interrupted with valleys, interspersed with scattered inselberg formations, probably caused by repeated cycles of tropical/wet morphoclimatic processes punctuated by drier periods over the last few million years (Ab'Saber, 2003; Safford and Martinelli, 2000). The study area also constitutes the headwaters for two important rivers, the Paraitinga and Mambucaba, which flow north and south, respectively.

2.2. Climate

The climate is categorised as tropical humid with seasonal precipitation (IBAMA, 2002). Annual average precipitation is 1670 mm, with ca. 40 mm in the driest month (July) and 265 mm in the wettest (January) (D1-022-Areias pluviometry station, http://www.hidrologia.daee.sp.gov.br, accessed 15 January 2018). Orographic precipitation from the Atlantic Ocean plays an important role as the Serra do Mar forms a barrier to easterly moisture. On the plateau, the temperature ranges from 29 to −4 °C and the annual average temperature is 17 °C, with mild, wet summers and cool, dry to moist winters (IBAMA, 2002; Nimer, 1977). The software NewlocClim (http://www.fao.org/nr/climpag/locclim/locclim_en.asp) estimates the mean maximum of the warmest month of 29.7 °C and the mean minimum of the coolest month of 7.6 °C. At the highest elevations, frost is common in the winter months, especially in high elevation basins. Increasing precipitation in southeastern Brazil since the Early Holocene is thought to be connected to gradual intensification of the South American Monsoon System (SAMS), which has resulted in higher austral summer insolation and a more southerly position of the Intertropical Convergence Zone in summer (Bernal et al., 2016).

2.3. Vegetation

IBAMA (2002) classifies the vegetation of the SBNP to three main ecosystems: campos de altitude, *Araucaria* forest and "Atlantic Forest" (referring to the various subzones and associated ecosystems that comprise the lowland and montane rainforest). The Bocaina Plateau itself is characterized by a mosaic of campos de altitude and *Araucaria* forest. The campos de altitude, which have clear modern human impacts, occupy the summits and the upper mountain slopes above 1500 m a.s.l. (Hiruma et al., 2012; IBAMA, 2002). The campos de altitude are rich in endemic species, predominantly characterized by non-arboreal species in the families Poaceae, Cyperaceae, Melastomataceae, Asteraceae, Ericaceae and Eriocaulaceae (Martinelli and Bandeira, 1989). Shrubby species of Asteraceae and Melastomataceae are dominant where the forest meets the grassland. *Araucaria* forest occurs as riparian forests as well as in small patches of forest surround by grassland between 1400 and 1800 m asl (IBGE, 2012). Important species of the *Araucaria* forest are *Araucaria angustifolia, Podocarpus lamberttii* and *Drimys brasiliensis*. The families Myrtaceae, Lauraceae, Fabaceae, Melastomataceae are common together with the tree ferns *Dicksonia sellowiana* (Dicksoniaceae) and *Alsophila capensis*

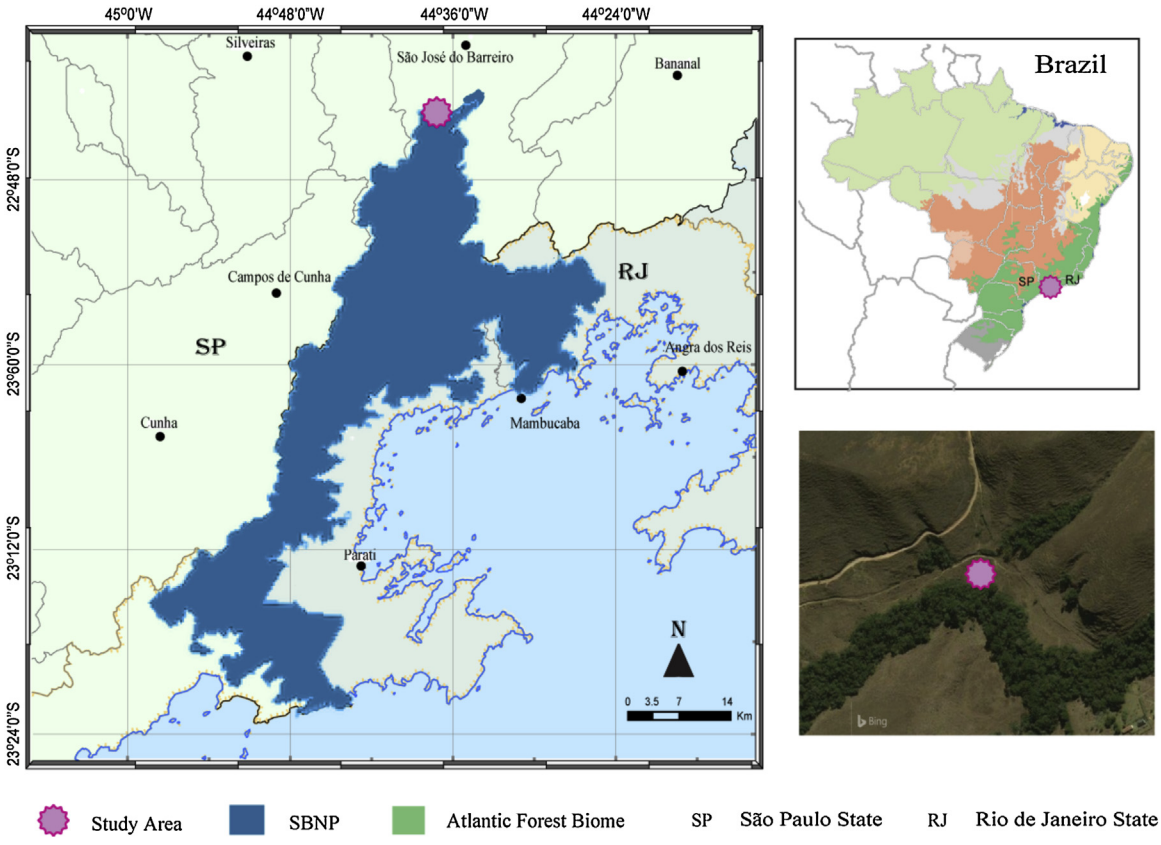

Fig. 1. Location of SBNP and the study site.

(Cyatheaceae) (IBAMA, 2002; IBGE, 2012). Apiaceae, Piperaceae and Rubiaceae characterize the forest shrub layer (IBAMA, 2002).

In the IBAMA classification, the Montane Atlantic Forest subzone is distributed between 700–1500 m a.s.l., on the mountain slopes, characterized by species of Lauraceae, Arecaceae, Fabaceae, *Cedrela fissilis*, *Luhea* sp., epiphytes and lianas. The Upper Montane subzone occurs in general above 1500 m a.s.l. in small fragments close to the mountain summits (IBAMA, 2002) characterized by the presence of fog, high humidity, low temperatures, strong winds and shallow soils (Portes, 2000). *Miconia*, *Weinmannia*, *Myrsine*, *Drimys*, *Clethra* and *Roupala* as well as the families Aquifoliaceae and Myrtaceae are common (IBAMA, 2002; Portes, 2000).

The swampy area from which the sediment was recovered is located near a small river and is covered by species of Poaceae and Cyperaceae. Surrounding the study site, the vegetation is a mixture of riparian forest with *Araucaria angustifolia* and *Podocarpus lambertii* and human influenced grassland, mostly used as a livestock pasture. The studied swamp is well preserved, without signs of disturbance and compaction as cattle access the pasture via paths that do not intersect the wetland.

2.4. Local history of human occupation

Several Amerindian groups inhabited the coast, mountains and inland territory around the Paraíba do Sul River valley over the last 8000 years (Bueno and Dias, 2015; Guidon, 1992). These were originally hunter-gatherers, but slash and burn agriculture began at least 1500 years before the arrival of Europeans (Corrêa, 2006; Noelli, 2008). Larger, more permanent settlements were mostly at lower elevations, but the nutritional value of *Araucaria* – and its high importance to Amerindians (Robinson et al., 2018) – suggests the possibility that there may have been some level of cultivation of this species on the Bocaina Plateau as well. Dean (1995) similarly suggests that the "islands" of *Araucaria* forest found in the southeastern highlands may not be totally natural, as they could have been planted in groups and protected from fire. Outside of major villages, native populations tended to be nomadic, typically moving every four years or so after exhausting the local land (Miller, 2000; Pádua, 2004). As a result, much of the landscape was comprised of secondary forest when the Europeans arrived. After European arrival, it is thought that up to 90% of the indigenous population died in the first hundred years of contact, which permitted some recovery of the forest during the early colonial period (Dean, 1995; Pádua, 2004).

The SBNP region was occupied by European settlers beginning in the middle of the 16th century, when small settlements were established along major indigenous pathways that crossed the forest. From these settlements, towns arose by the middle of the 17th century. Among these transportation routes, the "Caminho Novo da Piedade" was opened between 1725 to 1778 CE (André Bazzela, per. comm.). Today this route is highway SP-068, and connects the SBNP to the series of small towns and cities located along the inland escarpment of the Serra da Bocaina. Along the route, land was distributed to workers, who carried out subsistence agriculture and built extensions from the main road, further intensifying conflict with the native peoples (Antonio Filho, 2011).

During the coffee economic cycle (1800–1930 CE) several farmhouses were built on the Bocaina Plateau, among them the "Stone House" beside the study site, built in 1910 (Antonio Filho, 2011; IBAMA, 2002). The areas originally used for agriculture were burned and converted to coffee plantations (Almeida and Nötzold, 2008); after the decrease of coffee production in the region, most plantations were abandoned and converted to livestock pastures (IBAMA, 2002). Today, slash and burn is still a common practice to

promote the renewal of pasture and agricultural areas. Soils on the Bocaina Plateau are not highly fertile, and this practice tends to result in exhausted lands dominated by weeds after 2–3 years (Pádua, 2004) and a perpetuation of the expansion of secondary vegetation.

3. Material and methods

3.1. Sediment core and dating

In 2015, a 228 cm-long core was collected in an undisturbed swampy area in the SBNP using a Russian Corer. The core is called Serra da Bocaina Fazenda da Entrada (SBE). The stratigraphic description of the core was done using the Troels-Smith lithological symbols (Troels-Smith, 1955) and Munsell Colours System and the diagram was constructed in Psimpoll (Bennett, 1992).

Three samples were collected along the core for radiocarbon dating. Two samples (wood material) were sent to the AMS Laboratory at National Taiwan University (NTUAMS) and one sample (bulk) to the AMS Poznan Radiocarbon Laboratory (LAMS) (Table 1). A possible carbon reservoir effect can be excluded, as the test by HCl was negative. The age-depth model was performed with R script Clam version 2.2 (Blaauw, 2010) in R Studio (R Core Team, 2015) using the South Hemisphere calibration curve SHCal13.14C and postbomb curve SH 1-2.

3.2. Palynological analysis

A total of 39 samples of 0.5 cm^3 were taken along the core. Considering the sedimentation rate and lithological characteristics, in the lower core part (228–76 cm) samples were taken at 8 cm intervals and in the upper part (76-0 cm) in 4 cm intervals. Standard pollen preparation techniques were used to prepare the samples applying 40% hydrofluoric acid (HF) and acetolysis (Faegri and Iversen, 1989). One tablet with exotic *Lycopodium clavatum* spores as marker was added to each subsample prior to pollen extraction for the calculation of pollen concentration (grains/cm^3) and accumulation rate (grains/cm^2/yr) (Stockmarr, 1971). Slides were prepared with glycerol jelly for pollen taxa identification and counting under a light microscope up to a minimum of 300 pollen grains per sample. Identification is based on the reference collection of pollen and spores of the Department of Palynology and Climate Dynamics of University of Goettingen and literature (Behling, 1993; Melhem et al., 2003, Neotropical Fossil Pollen Search Tool developed by Dr. Hermann Behling and Dr. Chengyu Weng (unpublished)). Nomenclature follows the Flora do Brasil, 2018 (http://floradobrasil.jbjr.gov.br).

The pollen taxa exhibit in the diagram were classified in six ecological groups according to the habit and ecology of the taxa: Aquatics, campos de altitude (CDA), *Araucaria* forest (AF), Atlantic Forest (ARF) (Montane and Upper Montane), others (species that occur in all ecosystems) and ferns (ferns and tree ferns). Indeterminate, unknown, mosses and other Pteridophyta are excluded from the diagram as they were present at low percentages. The separation of the groups follows Behling et al. (2007) and modern vegetation surveys in southeastern Brazil (Freitas, 2010; Meireles et al., 2014; Ribeiro et al., 2013; Spolidoro, 2001).

The pollen sum did not include aquatic pollen taxa and spores. The pollen percentage diagram and summary diagram were developed with C2 (Juggins, 2007). Pollen assemblage zones were determined using stratigraphic constrained cluster analysis of the taxa forming the pollen sum by CONISS (Grimm, 1987).

A Principal Component Analysis (PCA) was performed with R Core Team (2015) using the package Vegan (Oksanen et al., 2017) to analyse the relationship among vegetation community composition. The PCA was carried out with pollen taxa with a relative abundance greater than 2% to maximize the signal to noise ratio. Data were centred and square root transformed prior to the ordination to minimize the effect of over-represented taxa in the record due to the difference in pollen productivity and dispersal rate among taxa (Prentice, 1980).

3.3. Macro-charcoal analysis

For analysing the past fire regime and its influence on vegetation, 1 cm^3 subsamples were extracted from the core at 1-cm resolution from 0 to 69 cm and 4-cm resolution from 69-228 cm. Lower sampling resolution was employed from 69 cm to the bottom of the core due to the higher sedimentation rate. Each sample was prepared following the method of Stevenson and Haberle (2005) adapted from Rhodes (1998). Weak hydrogen peroxide (6% H_2O_2) was added to remove organic material in the sediment. Samples were gently wet-sieved. All macro-charcoal particles >150 μm were counted under a binocular dissecting microscope. Concentrations were determined as particles/cm^3. The software CharAnalysis (Higuera, 2009) was applied to reconstruct the past fire regime characteristics. The charcoal raw data were interpolated according to the median temporal resolution (5 years) and converted into charcoal accumulation rates (CHAR particles/cm^2/yr). To separate background ($C_{background}$) and peak components (C_{peaks}), a 200-year window weighted regression robust to outliers was defined (Higuera et al., 2010). A Gaussian mixture model was used to identify the noise distribution (C_{noise}). Peaks greater than the 99th percentile threshold were identified as fire peaks. The Poisson minimum-count criterion was also used to eliminate the peaks from statistically insignificant counts. "Fire episode" frequencies over time were calculated based on the frequency of fire peaks per 200 years. Peak magnitude as an estimation of total charcoal deposition per fire event was used to reflect fuel consumption per fire and/or fire size (Biagioni et al., 2015; Higuera et al., 2010)

4. Results

4.1. Stratigraphy and chronology

The 228 cm-long sedimentological sequence shows 12 distinct deposits and can be grouped in three major sections. The largest

Table 1
AMS radiocarbon dates from SBE core, calibrated age ranges at 95% confidence intervals.

Lab-code	Depth (cm)	Material dated	Date (^{14}C age BP)	Calendar Age (cal yr BP)	Median probability (cal yr BP)
Poz-89783	38	bulk sediment	130 ± 30	−1 – 145 (77.5%) 222 – 260 (17.5%)	91
NTUAMS-2308	69	wood	355 ± 8	360 – 446 (82.5%) 319 – 334 (12.3%)	393
NTUAMS-2017	204	wood	607 ± 2	541 – 559 (93.3%) 619 – 621 (1.4%)	550

part of the core, from 228 to 76 cm consists of clayish-sandy material, mainly olive brownish in colour with poor pollen preservation. Within this section, at 205-200 cm, there is a layer of wood fragments with clay. The following section from 76 to 46 cm consists of brown clay/silt. An important change in the sediment occurs from 53 to 46 cm, within an interval from 50 to 47 cm in which siltier material is incorporated. The boundary with the uppermost section consists of a yellowish brown fine clay material. From 46 cm to the core top the sediment is comprised of brown organic somewhat clayey material, with the presence of roots, rootlets and plant remains. A complete detailed description of the stratigraphy can be found in the supplementary material.

The three Accelerator Mass Spectrometry (AMS) radiocarbon dates show that the SBE core reflects continuous sedimentation (Fig. 2). The smoothing spline age-depth model which provides better results for the data, indicates the core spans the last 600 cal yr BP (Fig. 2). The sedimentation rate decreases from the bottom to the top of the core (0.81-0.18 cm/yr). The lower section (228-70 cm) has a mean of 0.58 cm/yr, the middle section (69-38 cm) 0.22 cm/yr, whilst the uppermost section (37-0 cm) the rate is 0.19 cm/yr.

4.2. Palynological results

A total of 85 pollen and 36 spore taxa were identified in the 39 samples. The pollen diagram (Fig. 3) shows the dominant and most important taxa. The complete list of taxonomic groups can be found in the supplementary material.

The cluster analysis by CONISS resulted in four palynological zones: SBE-I, SBE-II, SBE-III and SBE-IV. The PCA ordination demonstrates that PC1 explains 36% of the variance and PC2 17%, after standardization of pollen data (Fig. 4). *Podocarpus* shows a strong correlation to PC1, whereas Poaceae is correlated with PC1 and PC2, although closer to PC1. Several taxa load more strongly on PC2, such as Moraceae/Urticaceae, *Mimosa scabrella*, Amaranthaceae and Mimosaceae. *Araucaria*, *Myrsine*, *Ilex* and Melastomataceae are placed very close to the origin, and their variance is not well explained by the first two PCA axes. The ordination separates four zones in accordance with the pollen diagram. Grass, herbs and some *A*F taxa are closely related to zone SBE-I. Following this zone, SBE-II is dominated by *Podocarpus*, with some connection to other *A*F taxa. In SBE-III, the dominance of *A*F taxa continues within species that represent both *A*F and Upper Montane ARF, and in SBE-IV Moraceae/Urticaceae is highlighted.

Pollen concentration varies from ca. 19,000 to 320,000 grains/cm^3 along the sediment core. Average values are 86,000 in zone SBE-I, 260,000 in SBE-II, 178,000 in SBE-III and 160,000 grains/cm^3 in zone SBE-IV (Figs. 3,5). Influx values range from 8000 to 160,000 per cm^2/yr. Average values are 56,000 in zone SBE-I, 670,000 in SBE-II, 37,000 in SBE-III and 30,000 per cm^2/yr in zone SBE-IV (Figs. 3,5). In the next section we describe each of the zones (all pollen percentages are averages).

4.2.1. SBE-I (228-88 cm; 600-350 cal yr BP; 1350–1600 AD) - 18 samples

The pollen assemblages are characterized by the highest values of CDA pollen in the core (44%, ranging from 35% to 55%), primarily represented by Poaceae (32%) and Asteraceae (9%). Pollen of Forest (48%, ranging from 35% to 60%) is slightly more abundant than CDA. *A*F (27%) is represented mainly by *Podocarpus* (10%) and *Weinmannia* (11%) while the ARF (8%) is represented mainly by Moraceae/Urticaceae (5%) and *Alchornea* (1.4%). *Araucaria angustifolia* pollen grains are found only in two samples. Other taxa (13%) are represented by Melastomataceae (6%) and Myrtaceae (5%). Cyperaceae shows the lowest values in this zone (<5%). Tree fern spores present their highest values in the core (3%), represented mainly by *Cyathea* (psilate form), as do fern spores (12%).

4.2.2. SBE-II (88-62 cm; 415-330 cal yr BP; 1540–1615 AD) - 5 samples

In this zone both Poaceae (16%) and Asteraceae (4%) are at core minima, contributing to the low value of CDA pollen (24%). The pollen assemblages are dominated by forest pollen (>70%), with the increase almost completely driven by an enormous increase in *Podocarpus* (38%). As a consequence, *A*F represents up to 52% of the pollen assemblages even with the decrease of *Weinmannia* (6%). *Symplocos tenuifolia* type (2%) and *Myrsine* (2%) are also important *Araucaria* forest taxa. Single grains of *A. angustifolia* occur in two samples. ARF (8%) is characterized by Moraceae/Urticaceae (4%) and *Alchornea* (3%). The group of Others (11%) is mostly composed

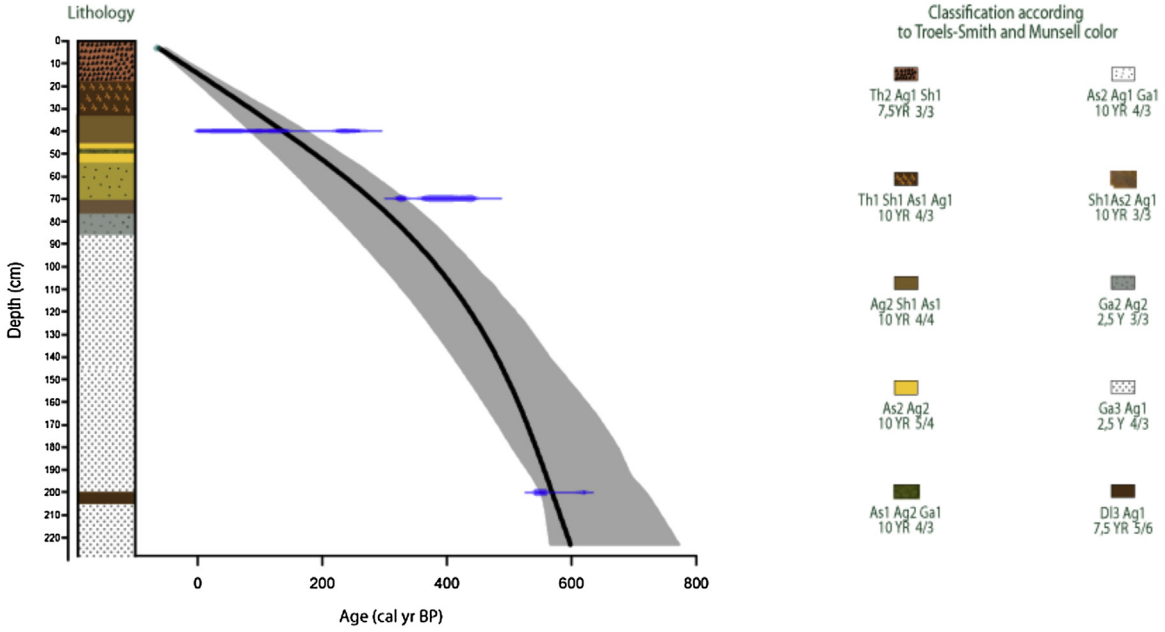

Fig. 2. Stratigraphy, characteristics of the sediment according to Troels-Smith (1955) and Munsell colour.

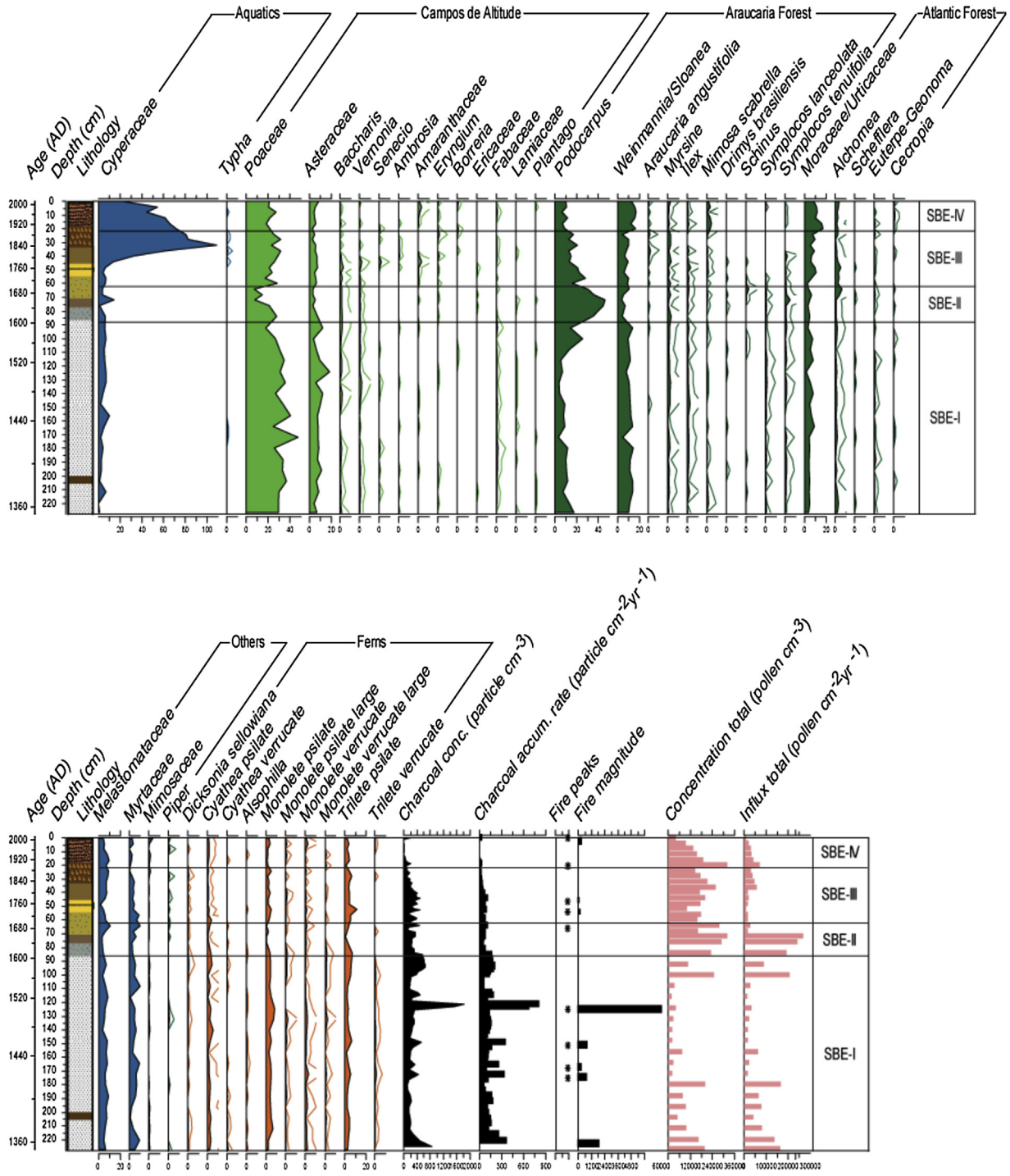

Fig. 3. Pollen percentage and charcoal diagram of SBE. A 5x exaggeration scale line is shown for low percentage values.

by pollen of Melastomataceae (5%) and Myrtaceae (5%). Cyperaceae shows a slight increase (6%) as do tree fern spores (2%).

4.2.3. SBE-III (62-22 cm; 330-35 cal yr BP; 1615–1920 CE) - 10 samples

Values of CDA pollen (36%), characterized largely by Poaceae (26%) and Asteraceae (6%), are higher than *AF* (32%), although Forest taxa still represent the main portion of the pollen assemblage (55%). Decrease in the *AF* assemblages is primarily due to the reduction of *Podocarpus* pollen (18%), though other *AF* taxa also decline such as *S. tenuifolia* type (0.6%) and *S. lanceolata* type (0.1%). Despite the low values of *AF* pollen, *A. angustifolia* shows the highest value in this zone (0.7%), as well as *Myrsine* (2%). The ARF assemblage increases continuously (11%), marked by Moraceae/Urticaceae (7%) and *Alchornea* (3%). Melastomataceae (6%) and Myrtaceae (4%) are the most abundant taxa in the group of Others (13%). There is a marked increase of Cyperaceae pollen (40%) after 1800 CE. Fern spores increase (10%), while there is a slight decrease of tree fern spores (1.7%).

4.2.4. SBE-IV (22-0 cm; 35 - -65 cal yr BP; 1920–2015 CE) - 6 samples

CDA pollen (31%) decreases slightly in this zone mainly as a result of lower Poaceae (22%) and Asteraceae (5%) values. Forest

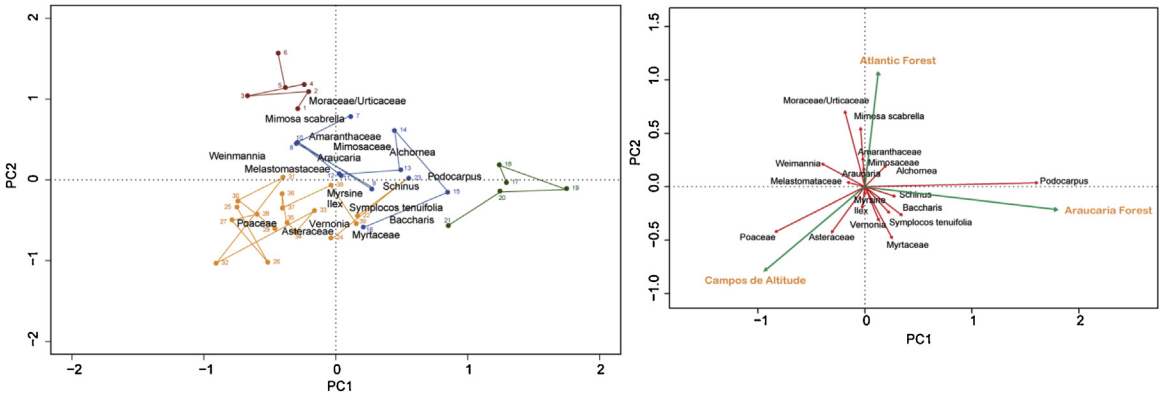

Fig. 4. Principal Components Analysis of the 18 most abundant species present at SBE.

taxa represent the main pollen group (57%). AF pollen maintains almost the same abundance as in the previous zone (30%). *Mimosa scabrella* (3%) and *Weinmannia* (15%), have the highest values, while *Podocarpus* decreases (9%). *A. angustifolia* also decreases and occurs only in three samples. ARF reaches its maximum value (17%) as Moraceae/Urticaceae achieves its highest average (12%) and pollen of the pioneer taxon *Cecropia* is more frequent (0.6%). The group of Others (11%) decreases slightly, characterized by Melastomataceae (6%), Myrtaceae (2%) and Mimosaceae pollen (1%). Cyperaceae pollen achieves maximum values (53%). There is a minor decrease of tree fern spores (1.5%) and a marked decrease of Ferns (7%).

4.3. Macro-charcoal and fire regime

The CharAnalysis of macro-charcoal shows an average concentration of 270 particles/cm^3 for the entire record, decreasing from zone SBE-I to SBE-IV (averages 370, 325, 260 and 50 particles/cm^3) (Figs. 3,5). Simultaneously, average charcoal accumulation rates also decrease from SBE-I to SBE-IV (Figs. 3,5). The local signal-to-noise is 5.1351, indicating a good separation between peak and non-peak values. The mean fire return interval (FRI, 95% probability) was 74 yr (38–114 yr). One fire episode failed to pass the Poisson minimum-count criteria (at 221 cm). Two of the three fire episodes occurred when the CDA summed pollen percentage was $\geq$40% and/or the forest sum pollen percentage was $\leq$50%. The highest concentration of particles is found at 121 cm of zone SBE-I (440 cal yr BP, 1510 CE); in this zone the highest magnitude fire peaks (> 100 particles per peak) are all found (Figs. 3,5). Zone SBE-I also supported the shortest mean FRI: including the fire episode at 221 cm, the mean FRI was about 40 years. Since 1720 the mean FRI has been about 71 years. The most recent peak fire event was detected at the uppermost 1 cm (2015-2007 CE).

5. Interpretation and discussion

5.1. Late holocene vegetation dynamics

The results from the studied environmental archive span the period from 1350 CE (150 years before the European arrival in Brazil) to 2015 CE. This record provides an opportunity to analyse human effects on vegetation composition and the differences between pre- and post-Columbian anthropogenic impacts and possible climatic influences.

Speleothem studies from Cristal Cave and Botuverá Cave, located 450 km and 700 km south from the study area respectively, show an increase in precipitation from the Early to Late Holocene in southern and southeastern Brazil (Bernal et al., 2016; Vuille et al., 2012). According to Vuille et al. (2012) the wettest period at Cristal Cave was between ~1600 to ~1820 CE. The sand and silty sediment from the bottom of the core until 76 cm (1350 to 1640 CE) suggests that colluvial and/or alluvial deposits formed this section of the soil. The shift to a more organic soil at 45 cm (1775 CE) may indicate a higher water table, which could be related to increasing precipitation as registered by Vuille et al. (2012), and/or to changes in local hydrology.

The general expansion of forest recorded in our core, as indicated by higher proportions of forest pollen like *Podocarpus*, *Weinmannia, Ilex, Myrsine,* and Melastomataceae relative to grassland vegetation, implies a trend toward wetter climate during the Late Holocene (Fig. 5). The increase in Atlantic Forest around 1900 CE (especially in Moraceae/Urticaceae and *Alchornea*) suggests the onset of warmer conditions in the last century coinciding with the Current Warm Period (CWP) (Vuille et al., 2012). The general rarity of *Araucaria angustifolia* in the core is also suggestive of warmer conditions characteristic of the Late Holocene. As background however, it is important to note that data from Behling et al. (2007) show that *Araucaria* has not been an abundant member of the high elevation forests in the Serra da Bocaina since at least 18,570 cal yr BP (beginning of the record). This is likely due to the lower and warmer environment in this tropical-marginal mountain site compared to much larger *Araucaria* populations in the higher and colder Serra do Mantiquiera and sites to the south.

After about 1520 CE and continuing to about 1670 CE, there is a marked and rapid increase in *Podocarpus* pollen, rising from near 10% to over 40%, followed by a similarly marked decrease to about 1720 CE. The coincidence of the first date with the period of European arrival in Brazil and rapid destruction of the Amerindian cultures and populations (Pádua, 2004), and the second date with the European settlement of the Paraíba do Sul Valley and the introduction of farming and livestock, suggest that forest expansion into grassland during this period may have been a result of a reduction in human activities. *P. lambertii* is a species of late secondary and climax forest, and typically found in dense, highly shaded and moist stands; it is rarely present in highly disturbed forest stands (Carvalho, 2004; Longhi et al., 2010). The lack of a positive response in fern pollen or ARF pollen during this time period argues against an increase in precipitation, further supporting the anthropogenic hypothesis. We interpret the reduction in Poaceae from 1600 to 1700 CE as a response to the expansion of forest. The expansion of forest after the arrival of the European settlers and the presence of more fire peaks and higher fire magnitude before 1520 CE further support the idea that pre-Columbian populations had important influence on the vegetation at the study site. Although lightning-ignited fires certainly occur in the Brazilian highlands (charcoal is found throughout pollen cores from campos habitat from well before Amerindian settlement of

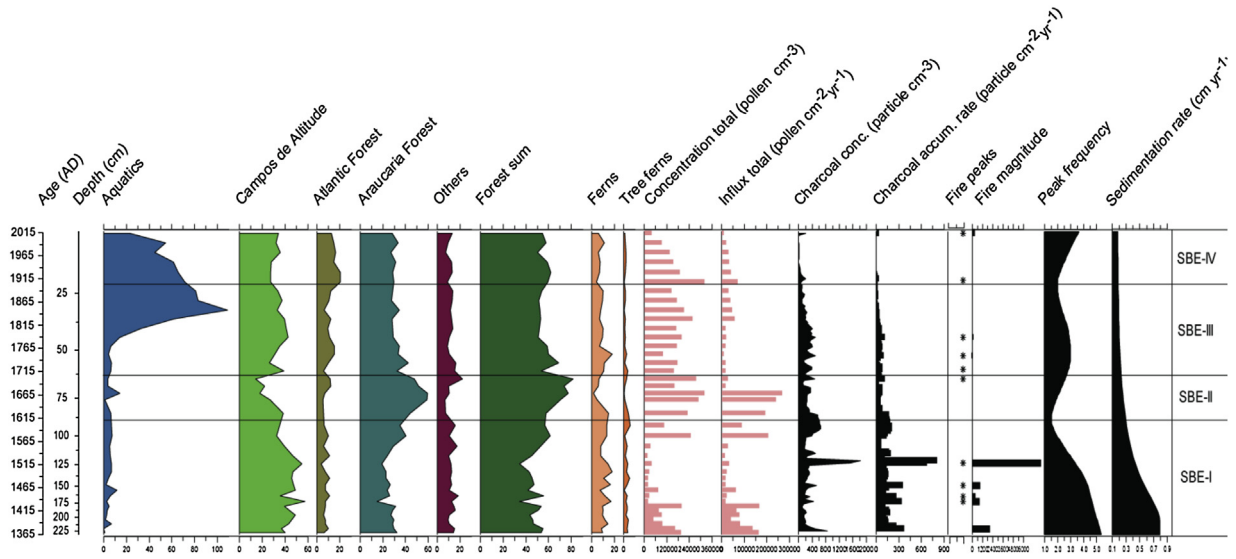

Fig. 5. Summary diagram of types of vegetation and macro-charcoal by age (AD).

the region, e.g. Behling, 1996; Behling et al., 2007), it seems likely that the pre-1500 extent of highland grassland-type vegetation at this relatively low site was influenced to some extent by human cutting and burning.

After 1680 CE, fire peaks begin to appear again, likely marking a new cycle of human influence on the local vegetation. Given the timing, we interpret the (slight) increase of grassland at this time as a result of renewed forest clearing and the introduction of cattle to the region. The sediment deposits also indicate a strong change (47–53 cm) overlapping the period when the Caminho Novo da Piedade was built between 1725–1778 CE. During this period, several minor roads/paths linking farms were established on the Bocaina Plateau, one of which passed close to the study site (it is still extant). We believe the construction of this path probably influenced the local water table and/or stream hydrology. The increase in Cyperaceae pollen after 1780 CE is due to a local rise in soil moisture and probably related to this change in hydrology, as is the increase in organic matter and plant remains in the core above 46 cm.

The increase in *Podocarpus* reversed by the late 18th century, and pollen percentages returned to a plateau (albeit a higher one than before 1520 CE). CDA pollen rebounded in return, but to a level fluctuating between 30% and 40%, rather than 40–50% as before 1520 CE. As noted above, the nature of the local depositional environment also rapidly changed at this time. Although local fires at the SBE site have not been very frequent in the last seven centuries (FRI = 74 yr, ranging from 38 to 114 yr), until the 20th century charcoal was constantly deposited at the site and background charcoal was present throughout the core, indicating that biomass was burning regionally. The near absence of charcoal from about 1910 CE (1887–1936 AD) to present, with only one peak fire event at 1 cm (2015–2007 CE) (Fig. 5), suggests that the 20th century expansion of forest in the study area may have to do both with increasing precipitation and a reduction in forest disturbance. There are late 20th century increases in a number of taxa indicative of early forest succession (e.g., both *Mimosa* pollen groups, *Cecropia*, Melastomataceae), providing further indication of a changed campos-forest dynamic.

5.2. The future of the campos-forest mosaic

The campos de altitude and similar mountain grasslands are highly species diverse and support many endemic and unique taxa (Martinelli and Bandeira, 1989; Overbeck et al., 2006; Rambo, 1953; Safford, 1999, 2007). It is clear from the paleoecological data that campos de altitude covered extensive areas of the southeastern Brazilian mountains during the LGM, and that cooling was sufficient to permit biogeographic connections with cold, temperate grassland habitats far to the south and southeast (Behling, 1996; Behling et al., 2007; Behling and Safford, 2010; Rambo, 1953; Safford, 2007). Today, after thousands of years of gradual warming and increasing precipitation, forest has "recovered" much of this area. Species diversity at the landscape scale is maximized by habitat heterogeneity – in this case, a forest-grassland "mosaic" (Bond and Parr, 2010; Overbeck et al., 2006) – and in the face of continued forest expansion, the maintenance of a forest-grassland balance is an important conservation goal in much of southern and southeastern Brazil (Behling and Pillar, 2007; Overbeck et al., 2015).

The balance between grasslands and forests in humid, tropical and subtropical environments is dependent on local or regional conditions that negatively influence the growth and/or competitive ability of woody plants. Such circumstances can include soil conditions (e.g. saturated soils or very thin or very nutrient-poor soils), cold and/or frost, and disturbance (Eiten, 1972; Smith, 1975; Van Langevelde et al., 2003). The campos de altitude sustains a flora dominated by species adapted to cold and to periodic fire (Safford, 1999, 2001). Fire occurred in the campos de altitude long before human settlement of Brazil (Behling, 1996; Behling et al., 2007; Verissimo et al., 2012), but it is also clear that anthropogenic disturbances – livestock grazing and logging as well as fire (Oliveira and Pillar, 2004; Pillar and Quadros, 1997) – have played a role in driving grassland-forest relationships in the southern and southeastern Brazilian highlands. Various studies have documented or postulated human agency in Late Holocene vegetation dynamics in the southern and southeast Brazilian mountains (e.g. Behling, 1996; Behling and Pillar, 2007; Bitencourt and Krauspenhar, 2006; Dean, 1995; Hueck, 1966; Robinson et al., 2018; Verissimo et al., 2012, this study). The broad expanse of campos de altitude during glacial periods was largely driven by much colder and somewhat drier climates, with help from periodic lightning-ignited fire. Today, the extent of campos de altitude is much reduced, but its current area is certainly larger than climate alone would dictate, especially in warmer, lower elevation sites like the Serra da Bocaina. Safford (2001) noted that frequent burning in what was originally upper montane forest leads to the presence of ruderal C_4 grasses like *Andropogon, Aristida, Axonopus,* and

Paspalum in lower elevation campos de altitude. Members of these genera are widespread in the Serra da Bocaina.

Annual mean temperatures in southeastern South America have risen about 1 °C over the last century, and projections suggest further increases of 2–3 °C by 2050 CE and 3–5 °C by 2080 CE, with greater seasonality in precipitation (which could lead to more dry season fire) and greater potential for heavy precipitation in the wet season (Marengo et al., 2009, 2012; Nuñez et al., 2009). Blanco et al. (2014) used a Dynamic Global Vegetation Model (DGVM) to predict a slight increase in the rate of forest expansion for the next decades, based on relative advantages for C_3 trees compared to C_4 grasses. Similarly, Behling and Safford (2010) suggested that future global warming was likely to intensify the upward movement of the Atlantic Forest at the expense of open ecosystems like the campos de altitude. Based on what we know about forest-grassland relationships in southeastern Brazil and what we know about current and projected climate trends, only two future scenarios seem reasonably plausible: eventual forest dominance in the absence of management, or forest-grassland coexistence in the presence of management (Blanco et al., 2014). Ensuring coexistence will require active management based on reference conditions and what we have learned about forest-grassland dynamics from both paleo- and modern ecological studies (Behling and Pillar, 2007).

Therefore, maintenance of much if not most campos de altitude habitat into the future will require (1) a change in conservation focus from forest to non-forest habitats, which runs counter to current policy emphasis in Brazil (Overbeck et al., 2015) and (2) serious consideration of active disturbance *management*, rather than disturbance *avoidance*, which is the current Brazilian National Park policy. In the SNBP and other conservation units protecting campos de altitude, we recommend the following steps (among others) be taken:

1 Carry out further studies to better elucidate the relative roles of anthropogenic and "natural" factors in driving the extent of campos de altitude and their relationship to neighbouring forested ecosystems. These include studies of both current and past conditions, and can range from high-resolution paleoecological studies, to comparisons of aerial photo-based time series, to empirical field studies (see next).
2 Carry out field research to better understand the effects of fire and grazing on successional processes, the forest-grassland balance, and key sensitive species in both grassland and forest habitats. Such research may be observational and opportunistic, but we especially recommend research and monitoring tied to the planned use of fire and grazing in controlled, experimental fashion, and the installation of areas that are protected from grazing (fenced exclosures), fire, and both grazing and fire. Experimental prescribed fire in campos de altitude has been recently implemented in Itatiaia National Park and we hope that this sort of "learning from managing" is soon extended to other conservation units.
3 Deploy remote data loggers to measure temperature and relative humidity patterns across the forest-grassland mosaic. After two to three years of data collection, use these data in combination with digital elevation models to map potential climate refugia for cold-adapted taxa. Such work is already underway in the Serra dos Órgãos National Park.
4 Develop a conservation assessment and conservation strategy for campos de altitude in southeastern Brazil. The conservation assessment would summarize information about the campos de altitude and key species and ecological processes across multiple spatial and temporal scales, with a focus on current and potential future threats. The assessment would serve as the foundation for a conservation strategy, which would provide science-based guidance for reducing threats to the campos de altitude and improving campos de altitude habitat quality and resilience.

Although Brazilian law directs that ecosystems protected by the national system of conservation units (SNUC) be managed "free of alterations caused by human interference" (Federal Law 9.985/2000), the same law also directs that management in the SNUC (1) contribute to the preservation and restoration of the diversity of natural ecosystems, and (2) recuperate or restore degraded ecosystems. Most Brazilian national parks are managed under the aegis of a management plan. In the case of SBNP, the use of fire is prohibited under any circumstances and livestock is considered an "interference" (IBAMA, 2002). At the same time, the main goal of the SBNP management plan is the protection of "natural vegetation", with a particular focus on ecosystems above 1500 m elevation (IBAMA, 2002), i.e. the campos de altitude-forest mosaic.

Major changes are underway in Brazilian national fire management policy, and the New Forest Code (Federal Law 12.651/2012) permits fire use in vegetation in the following cases:

1 Areas where local or regional peculiarities justify use of fire in agropastoral or forest settings (requires previous approval by applicable environmental agency)
2 Use of controlled fire in conservation units, conforming to a management plan and previously approved by conservation unit management agency
3 Scientific research activities carried out by recognized research institution and previously approved by applicable environmental agency

In addition, the New Forest Code also mandates (Article 40) that the Brazilian Federal government should establish a National Policy for Fire Management, Prevention, and Combat, including, among other things, fire management policy for protected natural areas. At this point in time, a draft policy document that effects a change from total fire suppression to a more nuanced, science-based approach of fire management has been written by IBAMA and partner agencies and is under consideration by the Brazilian Congress. Overall, it appears that there is already sufficient legal flexibility to experiment with fire in campos de altitude management, and such flexibility is likely to increase.

6. Summary and conclusions

We carried out a high-resolution paleoecological study of an almost 700-year core (1350–2015 AD) from the mosaic of *Araucaria* forest and campos de altitude in the Serra da Bocaina National Park, southeastern Brazil. We sought principally to elucidate interactions between the vegetation, climate and human activities before, during, and after arrival of Europeans in Brazil in the early 16th century. Our results demonstrate important changes in these interactions across this period of major cultural change. Amerindians had important impacts on the mountain vegetation, maintaining a more open habitat probably through slash and burn agriculture. After European arrival, the rapid depopulation of the study region plus increasing precipitation led to a strong rebound in forest cover, indicated principally by a four-fold increase in the pollen contribution of *Podocarpus*. After 1750, the establishment of permanent Portuguese communities and farming in the study area let to a renewed expansion of grassland, driven by land clearing, grazing, and anthropogenic fire.

Our results highlight the interworkings of regional climate change and local human agency in "designing" the Late Holocene forest-grassland mosaic in the Serra da Bocaina. Such forest-grassland mosaics are important contributors to landscape heterogeneity and biodiversity in southern and southeastern

Brazil. Given projections of continued warming into the future and the strong momentum such warming will lend to forest expansion, we recommend that Brazilian ecosystem managers consider transitioning from the current emphasis on passive management to a more active and experimental management agenda. We believe such an agenda is much more likely to answer the critical questions we have about how these important ecosystems might be sustained through the coming climate crisis.

Funding

This work was supported by the Ciências sem Fronteiras/CNPq program, Brazil (grant no 232876/2014-2) given to the first author.

Declaration of interest

None.

Acknowledgements

We gratefully acknowledge the ICMBio – Instituto Chico Mendes de Conservação da Biodiversidade, original institution of the first author, for allowing her in participating in the Program of Ecology and Biodiversity at University of Goettingen. We are thankful to ICMBio for given permission to developing this research in the SBNP. The field work would not be possible without the kindly support of the workers of SBNP, especially Mara Pais. We are very thankful to Dr. Vincent Montade, Dr. Siria Biagioni and Dr. Yoshi Maezumi for the discussions and insights. We are mostly indebted to the reviewers for their important comments and contributions.

Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.ancene.2018.11.004.

References

Ab'Saber, A.N., 2003. Os Domi'nios de Natureza No Brasil, In: Filho, Plínio Martins (Ed.), Potencialidades Paisagi'sticas. 4a. edição. Ateliê Editorial, São Paulo.
Almeida, C.S., Nötzold, A.L.V., 2008. O impacto da colonização e imigração no Brasil Meridional: contágios, doenças e ecologia humana dos povos indígenas. Tempos Acadêmicos 6. Unesc, Criciúma, SC.
Antonio Filho, F.D., 2011. Os caminhos dos Tropeiros e o Vale Histórico da Serra da Bocaina (SP): um espaço geográfico deprimido. Revista Geográfica de América Central, núm. esp. EGAL, pp. 1–20.
Behling, H., 1993. Untersuchungen Zur Spätpleistozänen Und Holozänen Vegetations- Und Klimageschichte der Tropischen Küstenwälder Und Der Araukarienwälder in Santa Catarina (Südbrasilien). (PhD thesis). J. Cramer, Berlin, Stuttgart.
Behling, H., 1995. Investigations into the Late Pleistocene and Holocene history of the vegetation and climate in Santa Catarina (S Brazil). Veget. Hist. Archaeobot. 4, 127–152.
Behling, H., 1996. Late Quaternary vegetation, climate and fire history from the tropical mountain region of Morro de Itapeva, SE Brazil. Palaeogeogr. Palaeoclimatol. Palaeoecol. 129, 407–422.
Behling, H., 1997. Late Quaternary vegetation, climate and fire history e Araucaria forest and campos region from Serra Campos Gerais, Paraná State (South Brazil). Rev. Palaeobot. Palynol. 97, 109–121.
Behling, H., 2007. Late Quaternary vegetation, fire and climate dynamics of Serra do Araçatuba in the Atlantic coastal mountains of Paraná State, southern Brazil. Veget. Hist. Archaeobot. 16, 77–85.
Behling, H., Pillar, V.D., 2007. Late Quaternary vegetation, biodiversity and fire dynamics on the southern Brazilian highland and their implication for conservation and management of modern Araucaria forest and grassland ecosystems. Philos. Trans. Biol. Sci. 362, 243–251.
Behling, H., Pillar, V.D., 2008. Vegetation and fire dynamics in southern Brazil during the late quaternary and their implication for conservation and management of modern grassland ecosystems. In: Schöder, H.G. (Ed.), Grasslands: Ecology, Management and Restoration. Nova Science Publishers, pp. 181–194.
Behling, H., Safford, H.D., 2010. Late-glacial and Holocene vegetation, climate and fire dynamics in the Serra dos Órgãos, Rio de Janeiro State, southeastern Brazil. Glob. Change Biol. Bioenergy 16, 1661–1671.
Behling, H., Pillar, V.D., Orlóci, L., Bauermann, S.G., 2004. Late Quaternary Araucaria forest, grassland (Campos), fire and climate dynamics, studied by high-resolution pollen, charcoal and multivariate analysis of the Cambará do Sul core in southern Brazil. Palaeogeogr. Palaeoclimatol. Palaeoecol. 203, 277–297.
Behling, H., Dupont, L., Safford, H.D., Wefer, G., 2007. Late Quaternary vegetation and climate dynamics in the Serra da Bocaina, southeastern Brazil. Quat. Int. 161, 22–31.
Bennett, K.D., 1992. Psimpoll: a quickBASIC program that generates PostScript page description files of pollen diagrams. INQUA Commission for the Study Of The Holocene: Working Group On Data Handling Methods Newsletter vol. 8, 11–12.
Bernal, J.P., Cruz, F.W., Stríkis, N.M., Wang, X., Deininger, M., Catunda, M.C.A., Ortega-Obregón, C., Cheng, H., Edwards, R.L., Auler, A.S., 2016. High-resolution Holocene South American monsoon history recorded by a speleothem from Botuverá Cave, Brazil. Earth Planet. Sci. Lett. 450, 186–196.
Biagioni, S., Krashevska, V., Achnopha, Y., Saad, A., Sabiham, S., Behling, H., 2015. 8000 years of vegetation dynamics and environmental changes of a unique inland peat ecosystem of the Jambi Province in Central Sumatra, Indonesia. Palaeogeogr. Palaeoclimatol. Palaeoecol. 440, 813–829.
Bitencourt, A.L.V., Krauspenhar, P.M., 2006. Possible prehistoric anthropogenic effect on Araucaria angustifolia (Bert.) O. Kuntze expansion during the Late Holocene. Rev. Bras. Paleontol. 9, 109–116.
Blaauw, M., 2010. Methods and code for 'classical' age-modelling of radiocarbon sequences. Quat. Geochronol. 5, 512–518.
Blanco, C.C., Scheiter, S., Sosinski, E., Fidelis, A., Anand, M., Pillar, V.D., 2014. Feedbacks between vegetation and disturbance processes promote long-term persistence of forest-grassland mosaics in south Brazil. Ecol. Modell. 291, 224–232.
Bond, W.J., Parr, C.L., 2010. Beyond the forest edge: ecology, diversity and conservation of the grassy biomes. Biol. Conserv. 143 (10), 2395–2404.
Bueno, L., Dias, A., 2015. Povoamento inicial da América do Sul: contribuições do contexto brasileiro. Estudos Avançados 29 (83), 119–147.
Carvalho, P.E.R., 2004. Pinheiro-Bravo: P. lambertii. Embrapa Florestas. Circular Técnica, pp. 95.
Corrêa, D.S., 2006. Historiadores e cronistas e a paisagem da colônia Brasil. Revista Brasileira de História 26 (51), 63–87.
Dean, W., 1995. With Broadax and Firebrand: the Destruction of the Brazilian Atlantic Forest. University of California Press, Berkeley.
Drummond, J.D., 1997. Devastação e Preservação Ambiental. Os parques nacionais do estado do Rio de Janeiro. Editora da Universidade Federal Fluminense, Niterói, RJ.
Eiten, G., 1972. The cerrado vegetation of Brazil. Bot. Rev. 38 (2), 201–341.
Faegri, K., Iversen, J., 1989. Textbook of Modern Pollen Analysis, 4th ed. John Wiley and Sons, Chichester.
Figuti, L., Eggers, S., Mendonça, C.A., Porsani, J.L., Rocha, E.B., De Blasis, P.A.D., Bissa, W.M., 2004. Investigações arqueológicas e geofísicas dos sambaquis fluviais do vale do Ribeira de Iguape, Estado de São Paulo. Museu de Arqueologia e Etnologia, USP. Relatório Final de Atividades de Projeto Temático, processo FAPESP nº 1999/12684-2, período: 6/2003 a 4/2004. .
Flora do Brasil, 2018. 2020 in construction. Jardim Botânico do Rio de Janeiro. . http://floradobrasil.jbjr.gov.br).
Freitas, H.S., 2010. Caracterizacao floristica e estrutural do componente arbóreo de três fragmentos de Floresta Estacional Semidecidual da região leste do vale do Paraíba (Master thesis). Instituto de Biociências da Universidade de São Paulo, São Paulo.
Fundação SOS Mata Atlântica/ INPE - Instituto Nacional de Pesquisas Espaciais, 2017. Atlas dos remanescentes florestais da Mata Atlântica - período. Relatório técnico., São Paulo, pp. 2015–2016.
Grimm, E.C., 1987. CONISS: a FORTRAN 77 program for stratigraphically constrained cluster analysis by the method of incremental sum of squares. Comput. Geosci. 13, 13–35.
Guidon, N., 1992. As ocupações pré-históricas do Brasil (excetuando a Amazônia), In: Cunha, M.C. (Ed.), História dos Índios no Brasil. 2ª ed. FAPESP, São Paulo, pp. 37–52.
Higuera, P., 2009. CharAnalysis 0.9: Diagnostic and Analytical Tools for Sediment-charcoal Analysis. User's Guide. Montana State University. http://CharAnalysis.googlepages.com.
Higuera, P.E., Gavin, D.G., Bartlein, P.J., Hallet, D.J., 2010. Peak detection in sediment-charcoal records? Impacts of alternative data analysis methods on fire-history interpretations. Int. J. Wildland Fire 19, 996–1014.
Hiruma, S.T., Modenesi-Gauttieri, M.C., Riccomini, C., 2012. Late Quaternary colluvial deposits in the Bocaina Plateau, southeastern Brazil highlands: age and palaeoenvironmental consequences. Boreas 42, 306–3016.
Hueck, K., 1966. Die Wälder Südamerikas. Ökologie, Zusammensetzung und wirtschaftliche Bedeutung. Gustav Fischer Verlag, Stuttgart.
IBAMA, 2002. Plano de Manejo do Parque Nacional da Serra da Bocaina available at. . http://www.icmbio.gov.br/parnaserradabocaina.
IBGE – Instituto Brasileiro de Geografia e Estatística, 2012. Manual Técnico da Vegetação Brasileira, 2nd edition IBGE, Rio de Janeiro.
Jeske-Pieruschka, V., Fidelis, A., Bergamin, R.S., Vélez, E., Behling, H., 2010. Araucaria forest dynamics in relation to fire frequency in southern Brazil based on fossil and modern pollen data. Rev. Palaeobot. Palynol. 160, 53–65.
Jeske-Pieruschka, V., Pillar, V.D., de Oliveira, M.A.T., Behling, H., 2012. New insights into vegetation, climate and fire history of southern Brazil revealed by a 40,000 year environmental record from the State Park Serra do Tabuleiro. Veget. Hist. Archaeobot. 22, 299–314.

Juggins, S., 2007. C2 User Guide: Software for Ecological and Palaeoecological Data Analysis and Visualization. University of Newcastle, Newcastle upon Tyne, UK, pp. 1–73.
Longhi, S.J., Brena, D.A., Ribeiro, S.B., Gracioli, C.R., Longhi, R.V., Mastella, T., 2010. Fatores ecológicos determinantes na ocorrência de Araucaria angustifolia e Podocarpus lambertii, na Floresta Ombrófila Mista da FLONA de São Francisco de Paula, RS. Brasil. Ciência Rural 40 (1), 1–7.
Marengo, JoséA., Jones, R., Alves, L.M., Valverde, M.C., 2009. Future change of temperature and precipitation extremes in South America as derived from the PRECIS regional climate modeling system. Int. J. Climatol. 29 (15), 2241–2255.
Marengo, J.A., Liebmann, B., Grimm, A.M., Misra, V., Silva Dias, P.L., Cavalcanti, I.F.A., Carvalho, L.M.V., Berbery, E.H., Ambrizzi, T., Vera, C.S., Saulo, A.C., Nogues-Paegle, J., Zipser, E., Seth, A., Alves, L.M., 2012. Recent developments on the South American monsoon system. Int. J. Climatol. 32, 1–21.
Martinelli, G., Bandeira, J., 1989. Campos de Altitude. Index, Rio de Janeiro. .
Meireles, L.D., Kinoshita, L.S., Sheperd, G.J., 2014. Composição florística da vegetação altimontana do distrito de Monte Verde (Camanducaia, MG), Serra da Mantiqueira Meridional, Sudeste do Brasil. Rodriguésia 65 (4), 831–859.
Melhem, T.S., Cruz-Barros, M.A.V., Côrrea, A.M.S., Makino-Watanabe, H., Silvestre-Capellato, M.S.F., Esteves, V.L.G., 2003. Variabilidade Polínica em Plantas de Campos do Jordão (São Paulo, Brasil). Boletim do Instituto de Botânica de São Paulo, São Paulo.
Miller, S.W., 2000. Fruitless trees: Portuguese conservation and Brazil's colonial timber. Stanford University Press, Stanford, California.
Myers, N., Mittermeier, R.A., Mittermeier, C.G., Fonseca, G.A.B., Kents, J., 2000. Biodiversity hotspots for conservation priorities. Nature 403, 853–858.
Nehren, U., Kirchner, A., Sattler, D., Turetta, A., Heinrich, J., 2013. Impact of natural climate change and historical land use on landscape development in the Atlantic Forest of Rio de Janeiro, Brazil. Anais da Academia Brasileira de Ciências 85 (2), 311–332.
Nimer, E., 1977. Clima. IBGE - Instituto Brasileiro de geografia e estatística. geografia do Brasil: região sudeste vol. 3, 51–90.
Noelli, F.S., 2000. A ocupação humana na Região Sul do Brasil: Arqueologia, debates e perspectivas-1872–2000. Revista USP, pp. 218–269.
Noelli, F.S., 2008. The Tupi expansion. In: Silverman, H., Isbell, W.H. (Eds.), Handbook of South American Archaeology. Springer, New York, pp. 659–670 Chapter 33.
Nuñez, M.N., Solman, S.A., Cabré, M.F., 2009. Regional climate change experiments over southern South America. II: climate change scenarios in the late twenty-first century. Clim. Dynam. 32 (7-8), 1081–1095.
Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P.R., OHara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Szoecs, E., Wagner, H., 2017. Vegan: Community Ecology Package. R Package Version 2.3-2. . https://CRAN.R-project.org/package=vegan.
Oliveira, J.M., Pillar, V.D., 2004. Vegetation dynamics on mosaics of Campos and Araucaria forest between 1974 and 1999 in Southern Brazil. Community Ecol. 5 (2), 197–202.
Overbeck, G.E., Müller, S.C., Pillar, V.D., Pfadenhauer, J., 2006. Floristic composition, environmental variation and species distribution patterns in burned grassland in southern Brazil. Braz. J. Biol. 66 (4), 1073–1090.
Overbeck, G.E., Vélez-Martin, E., Scarano, F.R., Lewinsohn, T.M., Fonseca, C.R., Meyer, S.T., Müller, S.C., Ceotto, P., Dadalt, L., Durigan, G., Ganade, G., 2015. Conservation in Brazil needs to include non-forest ecosystems. Divers. Distrib. 21 (12), 1455–1460.
Pádua, J.A., 2004. A ocupação do território Brasileiro e a conservação dos recursos naturais. In: Milano, M., Takahashi, L., Nunes, M. (Eds.), Unidades de Conservação. atualidades e tendências., Curitiba, pp. 12–20.
Pillar, V.D., Quadros, F.L.F., 1997. Grassland-forest boundaries in southern Brazil. Coenoses 12 (2-3), 119–126.
Portes, M.C.Gde., 2000. Deposição de serapilheira e decomposição foliart em Floresta Ombrófila Densa Altomontana, Morro do Anhangava, Serra da Baitaca, Quatro Barras - PR (Master thesis). Federal University of Paraná, Curitiba.
Prentice, I.C., 1980. Multidimensional scaling as a research tool in Quaternary Palynology: a review of theory and methods. Rev. Palaeobot. Palynol. 31, 71–104.
R Core Team, 2015. R Foundation for Statistical Computing Vienna, Austria. . http://www.R-project.org.
Rambo, B., 1953. A história da flora do planalto riograndense. Anais. Bot. Herb. Barbosa Rodriguez 5, 185–232.
Ribeiro, M.C., Metzger, J.P., Martensen, A.C., Ponzoni, F.J., Hirota, M.M., 2009. The Brazilian Atlantic Forest: how much is left, and how is the remaining forest distributed? Implications for conservation. Biol. Conserv. 142 (6), 1141–1153.
Ribeiro, T.M., Ivanauskas, N.M., Martins, S.V., Polisel, R.T., Santos, R.L.R., 2013. Fitossociologia de uma Floresta Secundária com Araucaria angustifolia (Bertol.) O. Kuntze na Estação Ecológica de Bananal, Bananal-SP. Floresta e Ambiente 20 (2), 159–172.
Rhodes, A.N., 1998. A method for the preparation and quantification of microscopic charcoal from terrestrial and lacustrine sediment cores. Holocene 8 (1), 113–117.
Robinson, M., De Souza, J.G., Maezumi, S.Y., Cárdenas, M., Pessenda, L., Prufer, K., Corteletti, R., Scunderlick, D., Mayle, F.E., Blasis, P., Iriarte, J., 2018. Uncoupling human and climate drivers of late Holocene vegetation change in southern Brazil. Sci. Rep. 8 (1), 7800. doi:http://dx.doi.org/10.1038/s41598-018-24429-5.
Safford, H.D., 1999. Brazilian páramos I. Introduction to the physical environment and vegetation of the campos de altitude. J. Biogeogr. 26, 713–738.
Safford, H.D., 2001. Brazilian Páramos III. Patterns and Rates of postfire Regeneration in the Campos de Altitude. Biotropica 33 (2), 282–302.
Safford, H.D., 2007. Brazilian páramos IV. Phytogeography of the campos de altitude. J. Biogeogr. 34, 1701–1722.
Safford, H.D., Martinelli, G., 2000. Southeast Brazil. In: Inselbergs: Biotic diversity of isolated rock outcrops. In: Barthlott, W., Porembski, S. (Eds.), Tropical and Temperate Regions. Ecological Studies No. 146. Springer-Verlag, Berlin, pp. 339–389.
Siqueira Ribeiro, M.C., Hackspacher, P.C., Ribeiro, L.F.B., Hadler Neto, J.C., 2011. Evolução tectônica e denudancional da Serra do Mar (SE-Brasil) no limite entre o Cretáceo Superior e Paleoceno, utilizando análises de traços de fissão E U-Th/He em apatitas. Rev. Bras. Geomorfol. 12 (3), 3–14.
Smith, J.M.B., 1975. Mountain grasslands of New Guinea. J. Biogeogr. 2, 27–44.
Spolidoro, M.L.C.V., 2001. Composição e estrutura em trecho de floresta no Médio Paraíba do Sul, RJ (Master thesis). Universidade Federal Rural do Rio de Janeiro, Rio de Janeiro.
Stevenson, J., Haberle, S., 2005. Macro Charcoal Analysis: a Modified Technique Used by the Department of Archaeology and Natural History. Palaeoworks Technical Papers 5, p. 7. Department of Archaeology and Natural History, Research School of Pacific and Asian Studies, Coombs Building. Australian National University, Australia ACT 0200.
Stockmarr, J., 1971. Tablets with spores used in absolute pollen analysis. Pollen et Spores 13, 615–621.
Troels-Smith, J., 1955. Karakterisering Af Lose Jordarter. Characterization of Unconsolidated Sediments. Danmarks Geologiske Undersogelse 4 (3), 1–73.
Van Langevelde, F., Van De Vijver, C.A., Kumar, L., Van De Koppel, J., De Ridder, N., Van Andel, J., Skidmore, A.K., Hearne, J.W., Stroosnijder, L., Bond, W.J., Prins, H.H., 2003. Effects of fire and herbivory on the stability of savanna ecosystems. Ecology 84, 337–350.
Verissimo, P.N., Safford, H.D., Behling, H., 2012. Holocene vegetation and fire history of the Serra do Caparaó, SE Brazil. Holocene 22, 1243–1250.
Vuille, M., Burns, S.J., Taylor, B.L., Cruz, F.W., Bird, B.W., Abbot, M.B., Kanner, L.C., Cheng, H., Novello, V.F., 2012. A review of the South American monsoon history as recorded in stable isotopic proxies over the past two millennia. Clim. Past Discuss. 8, 1309–1321.
Walker, M.J.C., Berkelhammer, M., Björck, S., Cwynar, L.C., Fisher, D.A., Long, A.J., Lowe, J.J., Newnham, R.M., Rasmussen, S.O., Weiss, H., 2012. Formal subdivision of the Holocene Series/Epoch: a Discussion Paper by a Working Group of INTIMATE (Integration of ice-core, marine and terrestrial records) and the Subcommission on Quaternary Stratigraphy (International Commission on Stratigraphy). J. Quat. Sci. 27 (7), 649–659.